

Inheritance Pattern of Metric Characters Affecting Grain Yield in Two Bread Wheat (*Triticum aestivum* L.) Crosses Under Rainfed Conditions

Zine El Abidine Fellahi^{1,2,*}, Abderrahmane Hannachi², Hamenna Bouzerzour³ and Abdelkader Benbelkacem⁴

¹Agronomy Department, Faculty of Life and Natural Sciences, Ferhat Abbas University, Setif 1, Algeria.

²Algerian National Institute of Agronomic Research (INRAA), Research Unit of Setif, Algeria.

³Ecology and Biology Department, Faculty of Life and Natural Sciences, LVRBN Laboratory, Ferhat Abbas University, Setif 1, Algeria.

⁴Algerian National Institute of Agronomic Research (INRAA), Research Unit of Constantine, Algeria.

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Abstract

The present investigation was undertaken to study the inheritance pattern and genetic analysis of some indicators of grain yield in F₁ and F₂ populations of two bread wheat crosses. The results reflected a satisfactory range of variability within and among the studied generations. Significant positive selection differentials were observed for all characters. High heritability estimates, coupled with high to moderate expected response to selection, were observed in most traits. High predicted genetic gain was observed for grain yield and above ground biomass. The estimated number of genes, involved in the genetic control of these characteristics, varied between 2 to 5, showing partial to over-dominance, suggesting that the selection must therefore be delayed until the F₄ or F₅ generation. Significant heterotic values in positive direction were found for all characters except thousand-kernel weight in both crosses and number of grains per spike in Acsad₈₉₉ × Mahon-Demias cross. Inbreeding depression was observed in both crosses for the number of spikes, above-ground biomass and grain yield. The obtained results indicated that the studied crosses would be of interest in the breeding program. It was suggested that the selection for all characters, except for thousand-kernel weight, should be effective in early segregating generations due to additive gene effects.

Keywords: Heritability, Heterosis, Potence ratio, Semi-arid, Wheat, Yield.

1. Introduction

In Algeria, bread wheat (*Triticum aestivum* L.) is one of the most important food crops. It is mainly grown in the northern part of the country under rain fed conditions (Fellahi *et al.*, 2013), where the production is subject to the fluctuation in the total yearly precipitation in addition to its distribution over the crop cycle (Chennafi *et al.*, 2006). Drought is a major limiting factor of cereal crops production, posing a serious threat to food security worldwide (Cattivelli *et al.*, 2008). Water deficit is a multidimensional stress affecting plants at various levels of their organization (Blum, 1996). When subjected to water deficit, wheat demonstrates various morphological,

physiological, biochemical, and molecular adaptive responses (Nezhadahmadi *et al.*, 2013). During the post-anthesis stage, drought reduces plant size, leaf area, grain filling duration, grain number, thousand-kernel weight and grain yield (Kaur and Behl, 2010; Nouri *et al.*, 2011). Physiological responses to water stress include stomata closure, development of oxidative stress, decrease in photosynthesis activity, alteration of the integrity of cell wall, production of metabolites to toxic levels, which cause plant death (Bray, 2002).

The genetic improvement of drought tolerance is an important objective in wheat breeding programs, in arid and semi-arid regions (Mullet and Whitsitt, 1996). Plant breeders need to develop varieties which are resilient to moisture stress conditions and able to express high grain

* Corresponding author. e-mail: zinou.agro@gmail.com.

yield potential (Noorka *et al.*, 2009). This requires a search for and a selection of traits such as biological yield, thousand-kernel weight, number of spikes, number of grains per spike and harvest index, which were found to be highly associated with grain yield (Richards *et al.*, 2002). Increasing the genetic potential of these traits is a continuous process. To accumulate a desirable gene pool in improved varieties, it is necessary to understand the mode of inheritance, the magnitude of gene effect and the mode of gene action in relation to the targeted environment for which varieties are to be developed (Farshadfar *et al.*, 2000). Previous genetic studies reported that both additive and non-additive gene actions were involved in the expression of most agronomic characters (Hannachi *et al.*, 2013). Nevertheless, the selection of promising parents to obtain superior hybrids depends, primarily, on the predominance of additive effect (Gowda *et al.*, 2010; Beche *et al.*, 2013). Keeping in view the importance of some metric characters as grain yield determinants under rain fed growth conditions, the goal of this research was to investigate the inheritance pattern of these metric traits in two bread wheat (*Triticum aestivum* L.) crosses utilizing P₁, P₂, F₁ and F₂ populations data sets.

2. Materials and Methods

2.1. Experimental Material and Design

The experience was carried out at the experimental field of the Algerian National Institute of Agronomic Research (INRAA), unit of Setif, during three successive crop seasons: 2010/11, 2011/12 and 2012/13. The experimental site coordinates are 36°15'N, 05°37'E and 981 m above sea level. In the 2010/11 cropping season, four genotypes Acsad₈₉₉, Mahon-Demias, Acsad₁₀₆₉ and Rmada were crossed to obtain F₁ seeds of the following crosses Acsad₈₉₉ × Mahon-Demias and Acsad₁₀₆₉ × Rmada. In the second season, the hybrid seeds of the two crosses were sown to grow the F₁ plants, which were selfed to produce F₂ seeds.

During the third season, seeds of four populations, P₁, P₂, F₁ and F₂, of each of the two crosses were sown in a randomized complete block design, with three replications. Plot had two rows of 10 m length, spaced 20 cm apart, with a plant to plant distance maintained at 10 cm by appropriate plant thinning. Ten competitive plants from parents, F₁ and thirty plants from F₂ generations were randomly harvested from each replication and measurements of above-ground biomass, thousand-kernel weight, spike number, number of grains per spike and grain yield were made.

2.2. Statistical Analysis and Estimation of Genetic Parameters

2.2.1. Variance Components, Heritability and Minimum Number of Genes

Estimates of phenotypic (σ_p^2), genotypic (σ_g^2) and environmental (σ_e^2) variances were obtained from the data of the parents and their offspring generations according to the method outlined by Cruz *et al.* (2012). Broad sense heritability (h_{bs}^2) was calculated using the

components of variance derived from the parental and the offspring generations' data according to Acquaah (2007).

$$h_{bs}^2(\%) = \frac{\sigma_g^2}{\sigma_p^2} \times 100$$

where, σ_g^2 = genotypic variance, σ_p^2 = phenotypic variance.

The minimum number of genes involved in the control of each trait was estimated according to Burton (1951).

2.2.2. Selection Differential and Expected Response to Selection

Selection differential (S), the expected response to selection (RS), the expected response to selection expressed as % of the base population mean (% RS) and the expected genetic gain (PGG) were calculated using the formulas reported by Cruz *et al.* (2012).

$$S = (\bar{X}_s - \bar{X}_o)$$

$$RS = S \times h_{rs}^2$$

$$RS(\%) = 100 \times \left(\frac{RS}{\bar{X}_o}\right)$$

$$PGG = (\bar{X}_o + RS)$$

2.2.3. Heterosis, potence ratio and inbreeding depression

The percent increase or decrease of F₁ hybrids over mid parent value was calculated to estimate heterosis, following Fonseca and Patterson (1968). The dominance estimate (P) was determined using the potence ratio method (Peter and Frey, 1966). Inbreeding depression (ID) was estimated by calculating the percent decrease of F₂ population mean over F₁ hybrid mean:

$$Heterosis = 100 \times \left(\frac{\bar{X}_{F1} - \bar{X}_{MP}}{\bar{X}_{MP}}\right)$$

$$P = 2 \times \left(\frac{\bar{X}_{F1} - \bar{X}_{MP}}{\bar{X}_{BP} - \bar{X}_{MP}}\right)$$

$$ID(\%) = 100 \times \left(\frac{\bar{X}_{F1} - \bar{X}_{F2}}{\bar{X}_{F1}}\right)$$

where \bar{X}_{F1} = the first generation mean, \bar{X}_{F2} = the second generation mean, \bar{X}_{MP} = mid parent mean, \bar{X}_{BP} = best parent mean. All statistical analyses were carried out using Genes software (Cruz, 2013) and Microsoft Excel spreadsheets.

3. Results

3.1. Mean Performances of the Evaluated Populations

Means and variances for the analyzed traits of the two crosses are presented in Table 1. Parents showed difference for all traits, in both crosses, except for thousand-kernel weight in Acsad₁₀₆₉ × Rmada cross. Mean values of the first filial generation of the Acsad₈₉₉ × Mahon-Demias cross were between parental values for the number of grains per spike. In both crosses, the performances of F₁'s were better than those of the best parents for the number of spikes per plant, above-ground biomass and grain yield. However, the F₁ mean performance of the number of grains per spike was higher than that of the best parent in Acsad₁₀₆₉ × Rmada cross only. Furthermore, F₁ generation showed significant

decline over respective parent for thousand-kernel weight in both crosses. These results indicated the presence of heterotic effects for these characters. Means of the second filial generations were between parental values for thousand-kernel weight, number of grains per spike, biomass per plant and grain yield in Acsad₈₉₉ × Mahon cross. F₂ population mean exceeded the mean of the best parent for number of spikes per plant in both crosses and for thousand-kernel weight, above-ground biomass per plant and grain yield in Acsad₁₀₆₉ × Rmada cross. These results indicated the presence of transgressive segregants in the F₂ generation for number of spikes per plant and thousand-kernel weight. Both traits are important determinants of grain yield, under semi-arid conditions. In addition, F₂ generation, of Acsad₁₀₆₉ × Rmada cross exhibited lower number of grains per spike than the lowest parent. The largest variances for all evaluated traits were found in the F₂ generation. These results were somewhat expected, since the observed variability of the F₂ generation is due to environmental and genetic sources (Falconer and MacKay, 1996).

Table 1. Means (\bar{X}) and variances (σ^2) for the studied characters of four wheat populations (P₁, P₂, F₁ and F₂) derived from two bread wheat crosses.

Generati on	Para meter	Characters				
		TKW	NS	NGS	BIO	GY
Acsad₈₉₉ × Mahon-Demias						
P ₁	\bar{X}	39.47	5.87	48.82	24.00	11.41
	σ^2	17.78	4.88	150.48	105.24	33.32
P ₂	\bar{X}	40.79	9.23	33.77	33.40	12.77
	σ^2	2.06	9.21	60.48	173.21	26.51
F ₁	\bar{X}	33.11	17.67	35.07	56.93	20.40
	σ^2	1.14	10.33	3.70	82.97	9.12
F ₂	\bar{X}	36.27	9.80	35.01	31.97	12.72
	σ^2	22.02	22.71	108.90	279.82	64.49
Acsad₁₀₆₉ × Rmada						
P ₁	\bar{X}	34.58	5.50	49.34	22.29	9.58
	σ^2	4.81	3.43	214.82	126.99	25.70
P ₂	\bar{X}	34.69	7.40	48.97	24.17	12.40
	σ^2	5.25	10.52	146.67	107.87	35.90
F ₁	\bar{X}	29.87	14.00	53.04	54.73	22.18
	σ^2	4.55	3.00	5.97	46.97	12.20
F ₂	\bar{X}	37.20	8.00	44.60	30.37	13.81
	σ^2	18.66	11.66	199.02	274.79	59.80

TKW: Thousand-kernel weight (g), NS: Number of spikes per plant, NGS: Number of grains per spike, BIO: Biomass per plant (g), GY: Grain yield per plant (g).

3.2. Variance Components, Heritability and Minimum Number of Genes

Estimates of the components of variance, heritability, potency ratio and the minimum number of genes are presented in Table 2. In the present study, the values of the components of genetic variance were generally greater than the environmental component of variance for all traits except the number of grains per spike in Acsad₈₉₉ × Mahon-Demias, where the two components are of similar

magnitude (Table 2). Therefore, the observed phenotypic variance can be associated, in most part, to the effect of their genetic differences, with negligible environmental effects. Contributions of genotypic variance to the total variance, in Acsad₈₉₉ × Mahon-Demias cross, were 74.9, 61.7, 49.9, 60.3 and 69.7 % for thousand-kernel weight, number of spikes per plant, number of grains per spike, above ground biomass and grain yield, respectively (Figure 1). These figures were 74.3, 57.2, 53.1, 70.1 and 64.0 % in Acsad₁₀₆₉ × Rmada cross for the above mentioned traits (Figure 1). In the present study, estimates of broad sense heritability ranged between 49.87 and 74.88 % (Table 2). Both low and high h²_{bs} values were observed in Acsad₈₉₉ × Mahon-Demias cross for the number of grains per spike and thousand-kernel weight, respectively. Generally, values of broad sense heritability were either equal to or greater than 50% for all characters understudy, indicating possibilities for improvement through selection in the genetic material produced.

The minimum number of genes is a useful indicator of the polygenic nature of the character studied. The minimum number of genes controlling thousand-kernel weight, spikes number, number of grains per spike, above ground biomass and grain yield in Acsad₈₉₉ × Mahon-Demias cross were 3.48, 2.90, 2.75, 4.86 and 4.85, respectively (Table 2). In the Acsad₁₀₆₉ × Rmada cross, these figures were 2.24, 4.21, 5.39, 2.82 and 3.47, respectively. These results indicated that the characters under study are controlled by a relatively small number of genes and a few selection cycles would be necessary to obtain the required accumulation of the favorable alleles controlling them.

Table 2. Estimates of phenotypic (σ_p^2), genotypic (σ_g^2) and environmental (σ_e^2) variance components, broad sense heritability (h²_{bs}), and minimum number of genes (mng) for the studied characters of four populations (P₁, P₂, F₁ and F₂) derived from two bread wheat crosses.

Genetic component	Characters				
	TKW	NS	NGS	BIO	GY
Acsad₈₉₉ × Mahon-Demias					
σ_p^2	22.02	22.71	108.90	279.82	64.49
σ_g^2	16.49	14.02	54.31	168.72	44.97
σ_e^2	5.53	8.69	54.59	111.10	19.52
h ² _{bs} (%)	74.88	61.74	49.87	60.30	69.72
F ₂ range	23.81/ 45.26	4.00/ 22.00	20.91/ 55.49	11.00/ 92.00	2.08/ 43.85
mng	3.48	2.90	2.75	4.86	4.85
Acsad₁₀₆₉ × Rmada					
σ_p^2	18.66	11.66	199.02	274.79	59.80
σ_g^2	13.87	6.67	105.67	192.59	38.30
σ_e^2	4.79	4.99	93.36	82.20	21.50
h ² _{bs} (%)	74.30	57.20	53.09	70.09	64.05
F ₂ range	29.67/ 45.44	4.00/ 19.00	13.34/ 80.87	9.00/ 75.00	2.37/ 34.99
mng	2.24	4.21	5.39	2.82	3.47

TKW: Thousand-kernel weight (g), NS: Number of spikes per plant, NGS: Number of grains per spike, BIO: Biomass per plant (g), GY: Grain yield per plant (g).

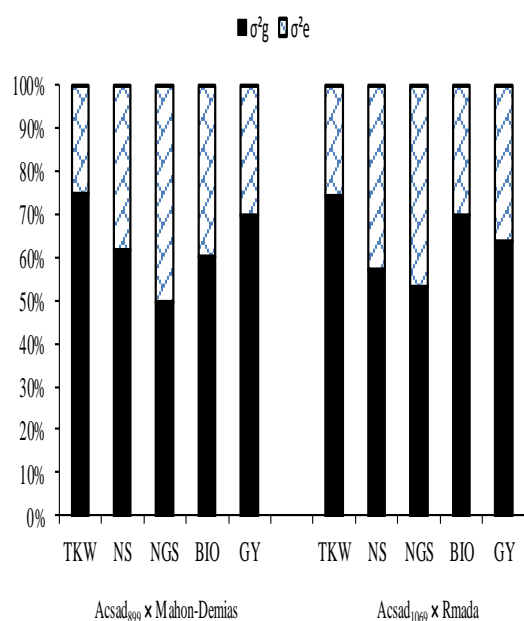


Figure 1. Relative contribution of the genetic and environmental variance components to the phenotypic variance for the measured traits in two bread wheat crosses.

3.3. Selection Differential, Expected Response to Selection and Expected Genetic Gain

The estimates of the selection differential for the studied characters ranged from 5.12 g for thousand-kernel weight in Acsad₈₉₉ × Mahon-Demias cross to 25.47 g for biomass per plant in Acsad₁₀₆₉ × Rmada cross (Table 3). Positive selection differentials indicate the possibility of selecting genotypes with good performances. Knowledge of the expected response to selection and the consequent expected genetic gain are essential to identify the appropriate selection criteria (Acquaah, 2007). In Acsad₈₉₉ × Mahon-Demias cross, values of the expected response to selection for thousand-kernel weight, number of spikes per plant, number of grains per spike, above-ground biomass and grain yield were 3.83 g, 4.96 spikes, 8.50 grains per spike, 14.99 g and 8.04 g, respectively. Expressed as a percentage, the expected response to selection for grain yield took the highest value of 63.25%, suggesting an expected genetic gain, after the first cycle of selection, of 20.77 g. The lowest value, 10.58%, of the expected response to selection, expressed as percentage of the mean of base population, was recorded for thousand-kernel weight, leading to an expected genetic gain of 40.09 g.

In Acsad₁₀₆₉ × Rmada cross, values of the expected response to selection for thousand-kernel weight, number of spikes per plant, number of grains per spike, above-ground biomass and grain yield were 4.51 g, 2.96 spikes, 9.08 grains per spike, 17.84 g and 7.21 g, respectively. The expected genetic gain values were 41.71, 10.96, 53.68, 48.21 and 21.02 for thousand-kernel weight, number of spikes per plant, number of grains per spike, above-ground biomass and grain yield, respectively (Table 3).

Table 3. Base population mean (\bar{X}_0), mean of the selected plants (\bar{X}_s), selection differential (S), expected response to selection (RS), expected response to selection expressed as percentage of the base population mean (%RS), and predicted gain genetic (PGG) for the studied characters of four populations (P₁, P₂, F₁ and F₂) derived from two bread wheat crosses.

Genetic component	Characters				
	TKW	NS	NGS	BIO	GY
Acsad ₈₉₉ × Mahon-Demias					
\bar{X}_0	36.27	9.80	35.01	31.97	12.72
\bar{X}_s	41.38	17.83	52.06	56.83	24.26
S	5.12	8.03	17.04	24.87	11.54
RS	3.83	4.96	8.50	14.99	8.04
RS (%)	10.58	50.61	24.27	46.90	63.25
PGG	40.09	14.76	43.51	46.96	20.77
Acsad ₁₀₆₉ × Rmada					
\bar{X}_0	37.21	8.00	44.60	30.37	13.81
\bar{X}_s	43.28	13.17	61.71	55.83	25.07
S	6.07	5.17	17.11	25.47	11.26
RS	4.51	2.96	9.08	17.84	7.21
RS (%)	12.11	36.93	20.36	58.78	52.20
PGG	41.71	10.96	53.68	48.21	21.02

TKW: Thousand-kernel weight (g), NS: Number of spikes per plant, NGS: Number of grains per spike, BIO: Biomass per plant (g), GY: Grain yield per plant (g).

3.4. Heterosis, Potence Ratio and Inbreeding Depression

Heterosis over mid-parent and inbreeding depression percentage values in both crosses are presented in Figure 2 for the studied characters. Positive heterosis values for the number of spikes per plant, above-ground biomass and grain yield were observed in both crosses. A positive heterosis estimate was also recorded for the number of grains per spike in Acsad₁₀₆₉ × Rmada cross. The heterosis values were low for grain yield and number of spikes but high for above ground biomass, in both crosses (Figure 2). Moreover, low and negative heterosis values were recorded for thousand-kernel weight in both crosses and for number of grains per spike in Acsad₈₉₉ × Mahon-Demias cross. Inbreeding depression was positive for number of spikes per plant, above-ground biomass and grain yield, and negative for thousand-kernel weight in both crosses (Figure 2). The maximum inbreeding effect was recorded for the number of spikes per plant in Acsad₈₉₉ × Mahon-Demias cross, while the minimum was exhibited by thousand-kernel weight in Acsad₁₀₆₉ × Rmada cross. The positive estimates indicated that mean values of the F₂ generation were reduced compared to F₁ means. The degree of dominance of the various traits, presented as potence ratio, is reported in Table 4. Thousand-kernel weight potence ratio absolute value was

greater than unity, in both crosses, suggesting over dominance. Over dominance acted in opposite directions, reducing this trait in $Acsad_{899} \times Mahon-Demias$ and increasing it in $Acsad_{1069} \times Rmada$ (Table 4). A partial dominance towards the higher parent was observed for the number of spikes per plant, biomass per plant and grain yield; and toward the lowest parent for number of grains per spike, in both crosses. Potence ratio absolute values of these traits were smaller than unity.

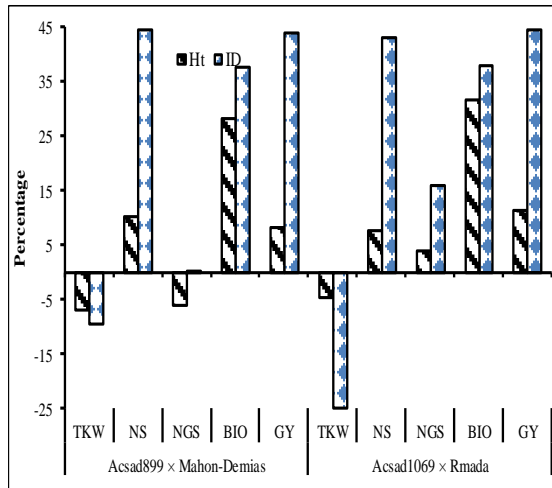


Figure 2. Percentage of heterosis (Ht) and inbreeding depression (ID) for the studied characters obtained in two bread wheat crosses.

Table 4. Potence ratio for the studied characters in two bread wheat crosses.

Characters	Potence ratio	
	$Acsad_{899} \times Mahon-Demias$	$Acsad_{1069} \times Rmada$
Thousand-kernel weight (g)	-2.75	2.24
Number of spikes per plant	0.60	0.36
Number of grains per spike	-0.33	-0.22
Above-ground biomass (g)	0.08	0.35
Grain yield per plant (g)	0.22	0.44

4. Discussion

Developing varieties resilient to moisture stress conditions and expressing high yield potential are an important objective in wheat breeding programs targeting arid and semi-arid regions. Various morphological, yield-related and physiological traits have been suggested as indicators for identifying drought tolerant genotypes (Richards *et al.*, 2002; Garcia del Moral *et al.*, 2003; Nouri *et al.*, 2011). The success of any plant breeding program depends on several factors including the amount of genetic variability, heritability and expected genetic gain of the trait under improvement. A higher amount of genetic variability accompanied by greater heritability and expected genetic gain will result in a significant progress

through selection (Nouri *et al.*, 2011). To accumulate a desirable gene pool in improved germplasm, it is essential to understand the extent of genetic variation and the inheritance pattern of the metric traits in relation to the targeted environment for which varieties are to be developed (Farshadfar *et al.*, 2000). The results of the present study indicated a large phenotypic variation between parents and filial generations for the analyzed traits. Genetic components were greater than the environmental component of variance, suggesting negligible environmental effects. Several researchers, reviewed by Mohamed (2014), reported a sizeable variability in wheat cross populations for agronomic traits.

The results indicated that F_1 's were better than the best parents for spike number, above-ground biomass and grain yield, suggesting the presence of heterotic effects. Transgressive segregants for thousand-kernel weight and inbreeding depression for biomass, grain yield, grains per spike and spike number were observed in the F_2 generation. Koumber and El-Gammaal (2012) reported similar results. Broad sense heritability values were equal to or greater than 50% for the traits under study, suggesting possibilities for improvement through selection. Heritability values, observed in this study, are of the same magnitude as those reported by Khan *et al.* (2007) and Khaled (2013). Knowledge of the heritability is important to breeders, because it measures the degree to which a character may be transmitted from parents to offspring and it indicates the extent to which the improvement is possible through selection (Acquaah, 2007). The studied traits are controlled by a relatively small number of genes, suggesting that few selection cycles would be necessary to obtain the required accumulation of the favorable alleles controlling them. The expected response to selection, expressed as a percentage of the base population mean, varied from 10.58% for thousand-kernel weight to 63.25% for grain yield.

Farshadfar *et al.* (2001) mentioned that moderate to high estimates of the expected response to selection suggest that the early selection could be effective as a strategy to improve the traits under study, whereas the delayed selection would be more effective to improve characters which exhibited a low expected response to selection values. Results indicated that over dominant inheritance was involved in thousand-kernel weight control, while partial dominance was involved in the genetic control of the other traits. Both additive and non-additive gene actions were involved in the expression of most agronomic characters (Hannachi *et al.*, 2013). Mohamed (2014) reported over dominance in the inheritance of these traits in two wheat crosses. Rashid *et al.* (2007) indicated that the grain yield was controlled by additive gene effects. Hassan *et al.* (2007) and Akhtar and Chowdhry (2006) reported that a partial dominance was involved in biomass, spike number and thousand-kernel weight.

The results suggested, based on h^2_{bs} , expected response to selection which expressed the significance of additive gene effects, that the early selection could be effective to improve the number of spikes, above ground

biomass, grain yield, and the number of grains per spike while delayed selection could be applied to improve thousand-kernel weight. In fact, a sizeable contribution of the dominance effect suggests postponing the selection of the character under improvement to advanced generations when a sufficient reduction of the dominance variance component is reached. However, in the presence of high dominance effect it is still possible to select superior plants in the progenies of a cross for a trait of interest.

5. Conclusion

In the present study, different characters were evaluated by estimating various genetic parameters in segregating and non-segregating generations in two bread wheat crosses under semi-arid environment. The results indicated the presence of desirable transgressors, in both crosses, for a number of spikes per plant; desirable transgressors for thousand-kernel weight, above-ground biomass and grain yield, and undesirable transgressors for number of grains per spike in Acsad₁₀₆₉ × Rmada cross. Estimates of broad sense heritability took intermediate to high values for all characters under study, expressing the significance of additive gene effects and indicating possibilities for improvement through selection. The expected response to selection varied among traits and was of a similar magnitude in both crosses. Over dominance was observed in the expression of thousand-kernel weight, and partial dominance was observed for a number of spikes, above-ground biomass, grain yield, and number of grains per spike, in both crosses. The results suggested that the early selection could be effective to improve the number of spikes, above-ground biomass, grain yield, and number of grains per spike while delayed selection could be applied to improve thousand-kernel weight.

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